Eurasia Specialized Veterinary Publication

Entomological Research Letters

ISSN: 3108-639X

2026, Volume 6, Issue 1, Page No: 41-50
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Available online at: www.esvpub.com/

Microclimate Sensing and Behavioral Buffering Can Scale from Individual Decisions to Geographic Persistence in Insect Populations

Patrick O'Connor[1]*, Grace Murphy[1], Niamh Walsh[2]

[1]Department of Microclimate Sensing and Behavioral Buffering, School of Biology, University College Cork, Cork, Ireland.
[2]Department of Geographic Persistence and Thermal Ecology, Faculty of Life Sciences, University of Galway, Galway, Ireland.

***E-mail** ✉ patrick.oconnor@ucc.ie

ABSTRACT

Climate exposure is often represented at spatial and temporal scales much coarser than those at which insects experience temperature, select microsites, alter activity, and complete reproduction. This creates an inferential gap between organismal thermal behaviour and population persistence. We develop a proposed scale-transition model in which geographic persistence is not inferred directly from thermoregulatory behaviour. Instead, persistence requires conditional transitions linking organism-relevant microclimate, temperature-contingent selection, physiological buffering, activity and reproduction, local demographic continuity, connectivity among usable refugia, and geographic colonisation–extinction balance. The evidence supports fine-scale thermal heterogeneity, taxon- and region-specific thermoregulatory behaviour, distinct behavioural and physiological buffering routes, and cases in which survival is maintained while reproduction is not. These findings make lethal-temperature avoidance an insufficient criterion for demographic buffering. The framework therefore treats each scale transition as an evidential gate rather than assuming that a beneficial response at one level propagates upward. Behavioral buffering can contribute to persistence only when suitable microclimates exist, can be detected and accessed, preserve performance across relevant life stages, and remain connected through time and space. Failure can therefore arise before physiological limits are crossed. The model is a testable ecological synthesis, not an empirically validated predictor of insect range persistence.

Keywords: Microclimate ecology, Behavioral thermoregulation, Thermal refugia, Insect demography, Climate buffering, Range persistence.

Received: 23 Month 2026
Revised: 15 Month 2026
Accepted: 18 Month 2026

How to Cite This Article: O'Connor P, Murphy G, Walsh N. Microclimate Sensing and Behavioral Buffering Can Scale from Individual Decisions to Geographic Persistence in Insect Populations. Entomol Appl Sci Lett. 2026;6(1):41-50.
https://doi.org/10.51847/U9xdOtGRvN

Introduction

Temperature is a dominant environmental axis in insect ecology, yet the evidence base is distributed unevenly across taxa, stages, and settings. A systematic map of butterfly research found extensive temperature-related work but strong concentration in adult and temperate systems, leaving stage, geographic, and taxonomic gaps that constrain generalisation [1]. The problem is therefore not simply whether temperature affects insects, but whether evidence collected at one biological or spatial scale can justify inference at another.

Microclimate provides the first scale distinction. Conditions experienced within vegetation, near surfaces, beneath canopies, or across small topographic features can differ substantially from regional or free-air climate, and these differences can propagate through ecological organisation [2]. For insects, the relevant thermal domain may be especially fine because small body size and close association with substrates place organisms within boundary

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layers and microsites that coarse meteorological observations do not resolve [3]. Consequently, “exposure” should not be treated as a single climatic variable shared by all individuals occupying a mapped grid cell.

A second distinction concerns sensing and behaviour. Temperature-dependent movement can arise from direct kinetic constraints as well as integrated behavioural responses to thermal information [4]. Observed position or activity therefore cannot automatically be labelled adaptive thermoregulation. Here, microclimate sensing is used operationally to mean ecologically detectable discrimination among thermal alternatives expressed through temperature-contingent positioning or activity, without implying a particular neural receptor pathway.

The ecological significance of microclimate becomes clearer only when it is connected to persistence. Fine-scale thermal heterogeneity has been associated with reduced climate-related regional extirpation risk, including for insects, showing that local climatic structure can modify broad-scale outcomes [5]. Conversely, long-term occupancy of cold-adapted Arctic and boreal butterflies has declined as minimum temperatures increased, demonstrating that broad warming can still erode distributional persistence despite local heterogeneity [6]. At the global scale, butterfly diversity and range-restricted lineages are concentrated disproportionately in mountain regions projected to experience substantial climatic exposure [7]. These studies motivate a cross-scale framework, but they do not demonstrate an uninterrupted causal chain from individual decisions to geographic persistence.

We therefore propose that scale-up should be evaluated as conditional evidential gates. Behavioral buffering may contribute to persistence when microclimatic alternatives are available, behaviourally usable, physiologically sufficient, compatible with activity and reproduction, demographically sustained, and spatially connected. Failure at any transition prevents inference from a lower-level response to a higher-level persistence outcome.

Materials and Methods

This article is an ecological framework. No new biological dataset, experiment, pooled effect estimate, or fitted predictive model was generated. The analytical procedure was to organize the approved evidence into sequential levels of inference while retaining explicit boundaries between physical exposure, behavioral selection, physiological performance, demographic consequence, and geographic outcome.

The first methodological rule is scale matching. Species-distribution models relying only on coarse climatic surfaces can misrepresent conditions actually experienced by organisms, whereas incorporating microclimate can improve ecological realism while introducing requirements for measurement and validation [8]. Landscape structure can also inform fine-scale climatic estimates through remote sensing, but remotely derived structure remains a proxy requiring calibration to the environmental variable and organismal process of interest [9]. High-resolution downscaling provides another route for recovering local climatic heterogeneity from broader data, although increased spatial resolution does not itself establish biological accuracy [10].

The second rule is that each scale transition requires an explicit evidential endpoint. Future insect-distribution studies vary substantially in model architecture, climatic inputs, and assumptions, and published projections include contractions and expansions rather than one universal direction of range change [11]. Geographic-range projections therefore cannot serve as the sole validation criterion for a framework beginning with organismal microclimate use.

The proposed Scale-Transition Model separates seven inferential states: local thermal opportunity, detectable exposure contrast, behavioral selection, physiological buffering, performance and reproduction, local demographic continuity, and spatially integrated geographic persistence. These states are neither numerical scores nor components assumed to multiply into a persistence probability. A transition is conceptually supported only when evidence appropriate to the higher level is available: behavioral observations cannot substitute for reproduction, physiological tolerance cannot substitute for population performance, and fine-resolution climate surfaces cannot substitute for movement or demographic connectivity.

Results and Discussion

Detection begins with the physical conditions available to an insect rather than an assumed sensory mechanism. Body size alters thermal coupling between insects and plant surfaces, so insects occupying the same nominal environment may experience different operative temperatures depending on size and boundary-layer context [12]. Free-air temperature is therefore an incomplete representation of the thermal alternatives from which behavior can operate.

Habitat structure further determines whether contrasting microclimates exist. In tropical forest, canopy disturbance was associated with a sharp erosion of microclimatic buffering relative to invertebrate thermal limits, illustrating that structural change can reduce thermal niche space within habitat [13]. The canopy values identified in that system are not transferable thresholds for other forests or insect groups, but the study demonstrates a boundary relevant to the proposed model: behavioral selection cannot buffer exposure if suitable alternatives have disappeared.

Accordingly, the framework distinguishes available microclimate from detectable microclimate. The former is a property of the physical environment at organism-relevant scale; the latter is inferred only when temperature-contingent positioning or activity indicates discrimination among available alternatives. This operational definition avoids equating physical heterogeneity with sensory use and avoids interpreting every temperature-correlated movement as adaptive choice because kinetic limitation can produce similar patterns [4].

Behavioral selection

Behavioral selection is the transition from thermally heterogeneous opportunity to realized use. Comparative butterfly studies show that thermoregulatory ability and mechanism vary among species, assemblages, and geographic settings rather than following a universal pattern [14–16]. In Britain, species differing in their reliance on microclimate selection also differed in associations with population trends [14]. In Catalonia, however, thermoregulatory ability did not explain regional demographic trends [15]. A standardized comparison across neotropical and temperate assemblages likewise found no consistent tropical–temperate hierarchy in thermoregulatory ability or mechanism [16]. Regional context and species identity must therefore bound any inference from thermoregulatory behaviour to vulnerability.

Thermal selection can also be temporal rather than spatial. Tropical butterflies in disturbed forest altered their activity schedules relative to counterparts in intact habitat, indicating that organisms may respond to altered microclimates by changing when activity occurs [17]. Such shifts demonstrate behavioral flexibility, but they do not establish fitness protection. Activity may be displaced into narrower daily windows or become separated from resources, mates, or otherwise favourable habitat conditions.

The proposed model therefore treats behavioral selection as an accessibility gate. A thermally favourable microsite has no buffering value if it is unreachable when required, incompatible with feeding or reproduction, or absent from the organism's movement domain. Behavioral selection is consequently neither synonymous with microclimatic heterogeneity nor sufficient evidence of adaptive benefit.

Physiological buffering

Behavioral buffering and physiological tolerance should remain analytically separate. In tropical butterflies, species-level thermal buffering and critical thermal maxima were negatively associated in the sampled assemblage, supporting the interpretation that different species can rely on different combinations of exposure avoidance and tolerance [18]. The result does not establish a universal evolved trade-off, but it shows why one dimension cannot safely substitute for the other.

Morphological traits are similarly incomplete substitutes for functional tolerance. In Sulawesi swallowtails, expected relationships among elevation, body size, and melanism were weak or absent, limiting the use of these traits as direct indicators of climatic vulnerability [19]. Morphology may influence heat exchange, but a morphological correlation is not equivalent to measured physiological performance.

Within the proposed Scale-Transition Model, physiological buffering is the capacity for organismal performance to remain within a usable range after realized exposure is determined. This definition separates the route by which exposure is modified from the physiological consequences of remaining exposure. It also requires stage specificity: tolerance measured in one stage cannot automatically be assigned to eggs, juveniles, pupae, or reproductive adults. Physiological buffering becomes relevant to persistence only when it protects functions contributing to subsequent survival and reproduction.

Activity and reproduction

The transition from individual thermal performance to demography is where simple buffering arguments can fail. In a plant-feeding treehopper, behavioral thermoregulation reduced exposure to lethal temperatures and enhanced survival, but reproduction was not equivalently maintained [20]. Survival buffering is therefore not a sufficient

proxy for population buffering. A thermal environment may remain nonlethal while becoming functionally unsuitable for mating, oviposition, development, or sustained activity.

Behavior can also impose opportunity costs. In the grain aphid, heat-avoidance behaviour altered microhabitat use and reduced demographic performance, showing that leaving a hot location can exchange direct thermal stress for reduced access to a host or other ecological costs [21]. Behavioral buffering should therefore be evaluated against resources required for performance rather than against temperature alone.

Life-stage and seasonal structure add another boundary. In the oriental fruit moth, responses to extreme high temperatures differed among developmental stages and seasonal cohorts, and short-term hardening did not erase this heterogeneity [22]. An adult-centered estimate of thermal tolerance or behavior may consequently fail to predict population effects when immobile or sensitive stages encounter different exposure regimes.

These findings motivate a proposed performance gate: behavioral and physiological buffering scale toward persistence only when they jointly preserve activities and vital rates required for population renewal. The gate is qualitative. It predicts that survival-only studies can overestimate demographic buffering when reproduction is more thermally restricted; that escape behavior can become costly when refuges are decoupled from food, hosts, or mates; and that population consequences depend on which life stage overlaps temporally with extreme exposure. These propositions require direct testing rather than numerical scoring.

Because these distinctions are readily collapsed in prose, the prediction-and-test ledger below keeps exposure avoidance, functional performance, and demographic inference analytically separate.

Table 1. Prediction-and-test ledger for determining when activity and reproduction permit thermal buffering to extend beyond individual survival

Interpretive limit and decisive check	Focal distinction with observed basis	Biological context with observed basis
Lethal exposure avoided and reproduction maintained		
Proposed transition criterion		
Other stages or seasons may remain limiting	Survival and reproductive buffering coincide	Reproductive insects using thermally heterogeneous habitat
Measure repeated vital rates across relevant stages	Individual buffering is compatible with demographic continuation	Body or operative temperature together with survival and reproductive performance
Lethal exposure avoided but reproduction compressed		
Evidence-grounded pattern		
Thermal performance windows are species- and context-dependent	Survival decouples from reproduction	Thermoregulating reproductive adults
Test reproduction within behaviorally selected microsites	Survival alone overstates demographic buffering	Survival remains possible while mating, oviposition, or reproductive output declines
Refuge use reduces access to hosts, food, or mates		
Evidence-grounded pattern		
Costs depend on refuge quality and resource distribution	Thermal benefit carries ecological opportunity cost	Host-associated or resource-limited insects
Quantify temperature and resource consequences jointly	Behavioral buffering can reduce net performance	Movement into cooler microsites coupled with resource-use or demographic change
Activity shifts toward cooler times		
Proposed test implication		
Resource or mate synchrony can change	Temporal selection substitutes for spatial relocation	Mobile adults in altered habitats
Couple activity timing with feeding, mating, and reproduction	Exposure may decline without demonstrating fitness protection	Diel activity timing changes with thermal conditions
A vulnerable stage remains exposed		
Evidence-grounded boundary		

Stage, cohort, and seasonal exposure differ **Sample stages overlapping the critical thermal event**	Stage mismatch in buffering Adult buffering cannot be assigned to whole-population persistence	Multistage life cycles Stage-specific survival, development, or later performance
	Buffering differs among seasonal cohorts ***Evidence-grounded boundary***	
Acclimation, season, and phenology can covary **Replicate across cohorts and seasons**	Temporal state dependence A single thermal estimate may misrepresent annual demographic consequences	Multivoltine or seasonally structured populations Cohort-specific thermal responses and vital rates

The same evidence requires a visual separation of physical opportunity, behavioral response, and fitness consequence. **Figure 1** places these processes on distinct biological layers and makes the survival-to-reproduction boundary an explicit scale-transfer checkpoint.

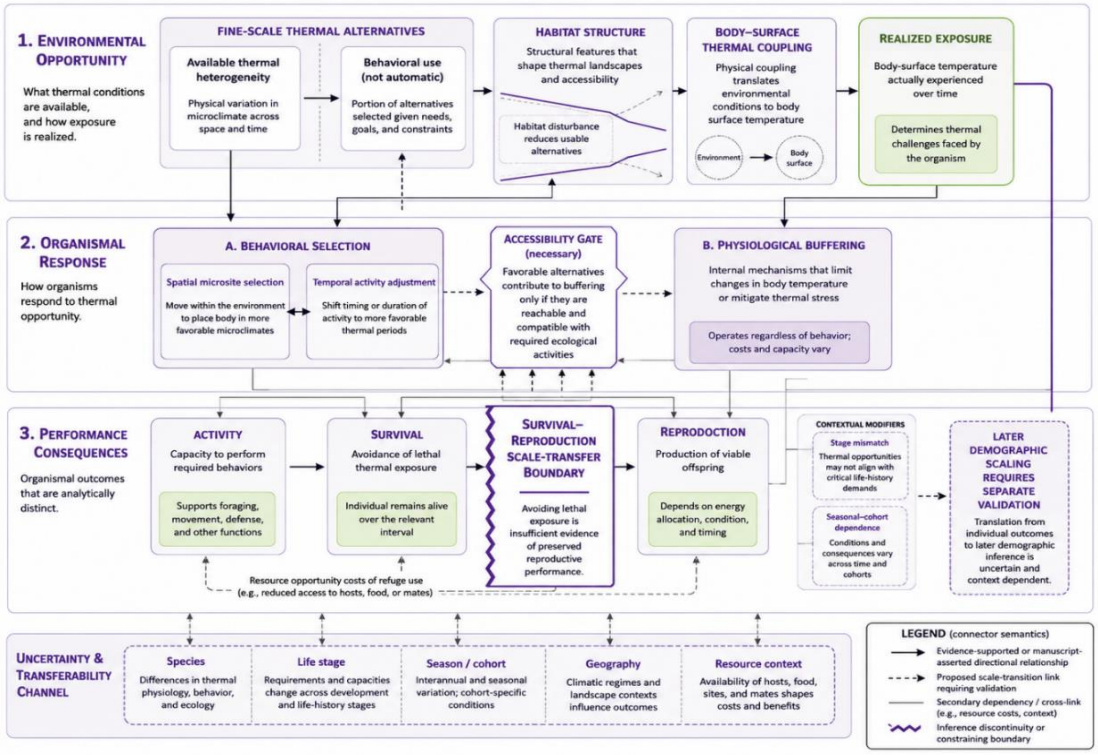


Figure 1. Survival can be buffered while the demographic pathway remains open to failure

Local population persistence

Local persistence is the first scale at which individual buffering must be translated into repeated demographic consequences. In Spanish mountain butterflies, habitat and microclimatic heterogeneity were associated with delayed community tracking of climate change, indicating that structurally complex landscapes can moderate the rate at which local assemblages reorganize [23]. A Mediterranean field study likewise recorded temperature-associated shifts toward wetter or shadier microsites, showing that fine habitat structure can remain behaviorally usable during hot conditions [24]. Neither result demonstrates indefinite population rescue: delayed tracking may reflect temporary buffering, colonisation limitation, or demographic inertia, while microsite use does not establish preserved reproduction.

Persistence also integrates climatic conditions outside the periods in which adult thermoregulation is most visible. Thirty-six years of montane butterfly monitoring linked population responses to warmer winters, snow conditions, and productivity, demonstrating that annual demographic outcomes can incorporate indirect and seasonal pathways not captured by summer body-temperature measurements [25]. A population may therefore experience effective daytime heat avoidance yet decline because another season, stage, or resource pathway limits recruitment.

The proposed framework defines local population persistence as repeated demographic continuity under realized exposure, not as the presence of thermoregulating individuals at one sampling time. This adds a temporal accumulation gate: buffering must preserve enough survival, development, reproduction, and recruitment across relevant stages and seasons for local occupancy to be renewed. Immigration can mask local failure, whereas short-term abundance can conceal delayed losses. Validation therefore requires repeated vital-rate or occupancy observations.

Landscape connectivity of refugia

A local refuge contributes to broader persistence only if organisms can reach suitable habitat as environmental conditions shift. Yet "connectivity" is not a single evidential category. A review of pollinator landscape-genetic studies found heterogeneous effects of landscape structure on genetic connectivity and emphasized that gene flow should not be treated as equivalent to demographic connectivity [26]. Genetic exchange may indicate historical or occasional movement without demonstrating that enough individuals move among thermal refugia at the right times to offset local losses.

Landscape context also modifies the climatic function of habitat. Multi-taxon mountain data show that macroclimate and microclimate can interact in shaping diversity, so the value of a cool patch cannot be interpreted independently of elevation, surrounding habitat structure, or the regional climatic envelope [27]. Refugia must therefore be understood as dynamic habitat states rather than fixed points on a map.

The proposed connectivity gate separates four questions: whether suitable refugia exist, remain suitable when needed, can be reached, and receive movement with demographic consequences. This prevents genetic connectivity, corridor continuity, and modeled habitat adjacency from being treated interchangeably. Temporal continuity also matters: a connection is ineffective if a refuge becomes unsuitable before movement or reproduction occurs.

The taxonomy/evidence decision matrix below separates these connectivity states because the same landscape can appear connected under one evidence class and functionally disconnected under another.

Table 2. Distinguishing refuge connectivity states before inferring demographic or geographic persistence

Focal distinction and warranted reading	Biological context with observed basis	Interpretive limit and decisive check
	Climatically suitable but isolated refuge	
	Proposed state	
Suitability without access **Local buffering need not scale beyond the occupied patch**	Species with limited movement or fragmented habitat Fine-scale thermal suitability with low observed interchange	Dispersal may be episodic or stage-specific Combine microclimate mapping with direct movement or repeated occupancy data
	Structurally connected habitat	
	Proposed inference boundary	
Physical continuity without demonstrated use **Potential route exists, but functional connectivity is unresolved**	Landscapes containing apparently continuous habitat Habitat adjacency, corridor structure, or remotely sensed continuity	Matrix permeability and behavioral avoidance may differ among taxa Test actual movement across the putative connection
	Genetic connectivity	
	Evidence-grounded boundary	
Gene flow without quantified demographic rescue **Movement has occurred across generations**	Pollinators or other insects assessed with population genetics Genetic similarity, assignment, or inferred gene flow	Historical movement may not match current demographic exchange Pair genetic evidence with contemporary movement and population trajectories
	Demographic connectivity	
	Proposed validation target	
Movement alters local population balance	Populations linked by dispersal	Direction, frequency, and stage of movement matter

Stronger basis for refuge-network persistence	Immigration, recruitment, colonisation, or rescue measured through time	Estimate whether movement offsets local losses under thermal stress
	Temporally synchronized refuge network	
	Proposed state	
Suitability and access overlap through time	Species tracking shifting thermal conditions	Refuges may fail asynchronously or resource conditions may diverge
Connectivity can support sequential use of refugia	Repeated microclimate suitability plus movement/occupancy through seasons or years	Test temporal overlap between refuge usability, movement, and reproduction

Figure 2 translates these distinctions into a temporal field because geographic persistence depends not simply on how refugia are arranged, but on whether climatic suitability, movement opportunity, and demographic continuity overlap through time.

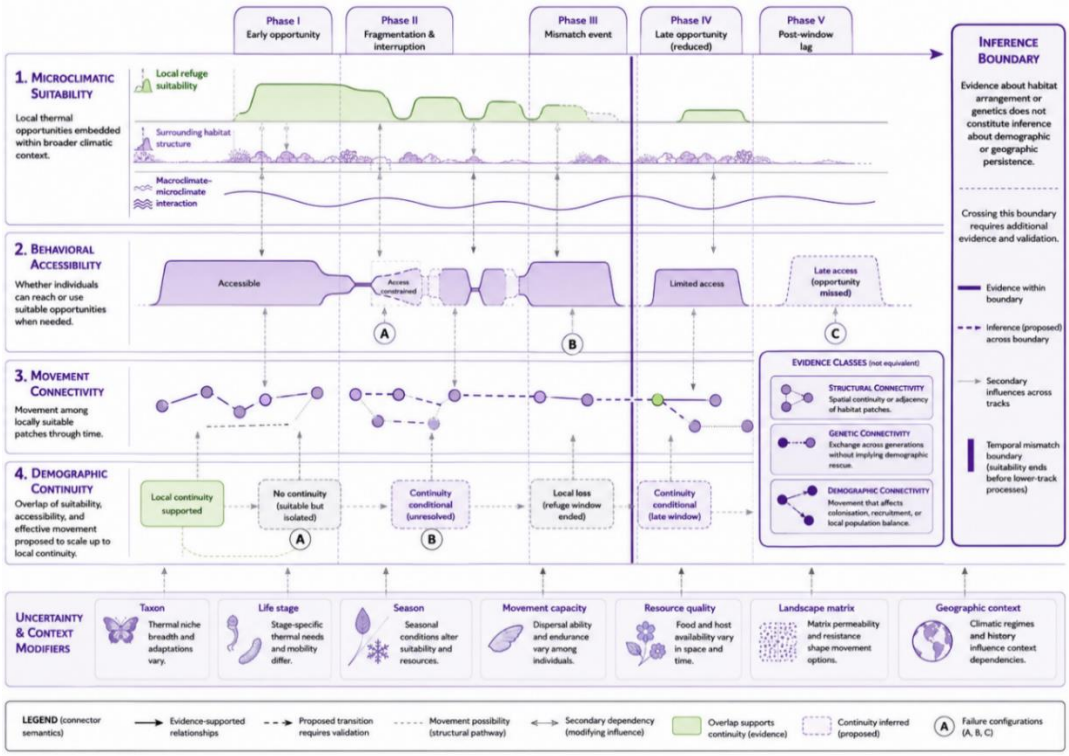


Figure 2. Refuge networks fail when climatic suitability, movement opportunity, and demographic continuity become temporally misaligned

Geographic range persistence

Geographic persistence should not be equated with an unchanged range boundary. In Puerto Rican butterflies, climate-based ensemble models projected taxonomic and functional homogenisation, illustrating possible geographic reassembly rather than an observation of future persistence [28]. Such projections remain conditional on climate, dispersal, biotic interactions, and the relationship between modeled suitability and realized occupancy. Repeated surveys provide a more direct bridge between local climatic conditions and regional change. In central Spanish mountain butterflies, local climate was associated with colonisation and extinction patterns that altered community thermal composition [29]. Colonisation by warmer-affinity taxa and losses of cooler-affinity taxa demonstrate how geographic reorganization can emerge from local turnover, while still leaving the individual mechanisms of movement and buffering partly unresolved.

Continental bumble-bee records similarly show thermal restructuring of North American communities with summer warming, including declines of colder-associated taxa and increases of warmer-associated taxa [30]. These data support broad-scale reassembly but do not identify behavioral buffering as the sole cause of persistence

or decline. The proposed framework therefore defines geographic persistence as maintenance of occupancy across a shifting network of local populations, potentially including redistribution. Static range position is only one possible outcome.

Failure thresholds

Failure is not restricted to crossing a lethal physiological limit. Habitat disturbance can first remove the thermal alternatives on which behavioral buffering depends [13]. Even where refugia remain, survival may be maintained while reproduction is not [20], or heat avoidance may impose demographic costs through reduced resource access [21]. Stage- and cohort-specific thermal responses further mean that a population can fail through a vulnerable life stage despite apparently robust adults [22].

The proposed framework recognizes four qualitative failure classes. Availability failure occurs when suitable microclimates disappear. Performance failure occurs when refugia prevent lethal exposure but not activity or reproduction. State mismatch occurs when buffering measured in one stage, season, or cohort fails to represent another. Scale-transfer failure occurs when local buffering cannot propagate through movement, demographic connectivity, or geographic inference.

Methodological failure must be kept separate from biological failure. Insect range forecasts vary substantially among modeling approaches and assumptions [11], while landscape-genetic connectivity does not by itself establish demographic rescue [26]. A model can therefore fail to predict persistence even when biological buffering exists, and a biologically plausible refuge network can remain unvalidated when the evidence measures only structural or genetic connectivity. No universal numeric threshold is justified across these classes.

The central argument is not that microclimate buffering guarantees insect persistence, but that persistence can be decomposed into testable transitions that are too often conflated. The literature is rich in temperature studies yet uneven across stages, regions, and taxa [1], while microclimate ecology still identifies scaling from local conditions to broader ecological outcomes as a major challenge [2]. The proposed framework organizes that gap without treating it as already solved.

Behavioral thermoregulation is particularly unsuitable as a universal vulnerability index. British butterflies showed an association between thermoregulatory strategy and population trends, whereas the corresponding relationship was absent in Catalonia [15]. Regional climate, habitat structure, species identity, and available microhabitats can therefore alter the meaning of the same behavioral metric. The framework accordingly treats behavior as one conditional gate rather than the mechanism that determines persistence.

Fitness validation should also extend beyond mortality. Experimental evidence that survival can be buffered without equivalent reproductive protection demonstrates why lethal-limit endpoints may overestimate demographic resilience [20]. Future tests should pair operative or body temperatures with stage-specific activity, reproduction, development, and recruitment. Where avoidance changes resource access, the ecological costs of refuge use should be measured simultaneously rather than assumed negligible.

The transition from local persistence to geography requires equally careful evidence. Colonisation and extinction observations provide a closer demographic bridge to range change than static suitability maps [29], whereas genetic connectivity can document exchange without establishing contemporary demographic rescue [26]. Strong validation would therefore combine organism-scale microclimate, observed behavior, physiological performance, vital rates, repeated occupancy, direct movement, and colonisation–extinction dynamics across the same study system.

Geographic persistence may manifest as stability, redistribution, or community reassembly. Modelled future homogenisation in butterflies [28] and observed thermal restructuring in bumble-bee communities [30] belong to different evidence classes and should not be collapsed. The former describes a projection under specified assumptions; the latter documents historical change but does not isolate a single mechanism. Preserving this distinction is essential when using the framework for conservation inference.

Several boundaries remain. Butterfly studies dominate the behavioural and field evidence, experimental demographic examples come from few non-butterfly systems, and adult measurements exceed whole-life-cycle tests. Sex-specific responses are insufficient for general rules. Refugia can also differ in food or host quality, while density dependence and biotic interactions can alter persistence independently of temperature. The framework should therefore be tested comparatively rather than treated as universally parameterized.

A decisive validation design would follow populations across scales: measure organism-relevant microclimates; document temperature-contingent choices; quantify physiological performance; measure survival and

reproduction across vulnerable stages; estimate local demographic continuity; determine whether refuge movement is demographically consequential; and relate colonisation and extinction to regional occupancy change. Such work could identify which transitions fail most often across insect life histories. Until then, the framework remains an evidence-organizing, hypothesis-generating architecture.

Conclusion

T Microclimate can alter the thermal world available to insects, but geographic persistence cannot be inferred from local heterogeneity or thermoregulatory behavior alone. The proposed scale-transition model separates physical opportunity, behavioral selection, physiological buffering, performance, reproduction, demographic continuity, refuge connectivity, and regional turnover into distinct evidential gates. This structure explains how buffering may succeed at one level yet fail at the next, including cases where survival persists while reproduction, recruitment, movement, or habitat continuity does not. It also accommodates redistribution rather than requiring geographic stasis as the definition of persistence. The framework is therefore best treated as a testable ecological architecture for linking scales, with validation requiring coordinated measurements from organismal microclimate through population turnover rather than stronger inference from any single proxy.

Acknowledgments: None

Conflict of Interest: None

Financial Support: None

Ethics Statement: None

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